Vertical distribution of Collembola in a *Pinus nigra* organic soil

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Summary. The vertical distribution of some abundant Collembola species in a coniferous
forest soil was studied for 2.5 years. with summer and winter sampling. Enclosures were
used to manipulate the presence of live tree roots and other soil fauna. in order to study
their effects on the depth stratification of these species. Mean depths and depth deviations
(Usher 1970) were expressed as relative measures. related to rank numbered subsamples
of the soil core by fresh litter. fragmented litter and humus layers. The various Collembola
species. viz. *Isotoma notabilis*. *Neanura muscorum*. *Neelus minimus*. *Lepidocyrtus cyaneus*.
L. lignorum. *Orchesella cincta* and *Tomocerus minor* showed specific mean relative depths
with partial overlap between species. The mean relative depths of these species varied
between 1.29–1.67 cm. which is equivalent to an average of 2.2–2.8 cm actual depth.
Mean relative depths and relative depth deviations varied with body size. Litter moisture
content. leachate acidity. and the presence of other soil fauna and live tree roots affected
depth distributions of Collembola species in a species-specific way. The method used to
measure relative vertical distributions is discussed.

Key words: Collembola. vertical distribution. coniferous forest soil. habitat utilization.
resource partitioning. body size

Introduction

From a community ecological point of view. the study of depth stratification of soil animals
may provide insight into the mechanisms for avoidance of interspecific competition between
species. Thus. resource partitioning in Collembola may be established by vertical micro-
habitat utilization (Takeda 1987). in addition to separation along horizontal gradients
(Rusek 1979; Joosse 1981) and seasonal resource partitioning (Vegter 1987). The study of
depth stratification may also reveal predator niche dimensions (Huhta 1971; Kessler &
van der Ham 1988). In a system ecological sense. the contribution of soil fauna to
decomposition and nutrient cycling may be better understood given knowledge on the
vertical distribution of individual species (Faber 1991a). The specific roles of collembolans
and other soil fauna are hypothesized to be related to their vertical distribution in soil
(van Straalen et al. 1985; Faber 1991a; Faber & Verhoef 1991). The testing of this
hypothesis requires further information on microstratification of soil invertebrates. Prefera-
bly then. such investigations should run parallel to an elucidation of the role of soil fauna
in decomposition processes that uses an experimental approach.
The present paper presents data on microstratification of seven species of litter dwelling
Collembola. abundant in a coniferous forest soil. The stratification of the fauna was studied

in relation to pedomorphological strata, therefore the soil organic layer was subsampled for the litter layers and humus. After description, the stratification patterns of Collembola species were specified for individual body length, and specific patterns of vertical distribution were analysed for seasonality and for relationship with the presence of other Collembola species, and some edaphic factors: soil moisture, soil acidity, and the presence of live pine tree roots. The data were collected during an experiment, set up to study the long-term impact of individual Collembola species on litter decomposition and mineralisation in relation to depth distribution (Faber 1991b; Faber & Verhoef 1991).

Materials and Methods

Site description

The experiment was situated in a *Pinus nigra* Arnold var. *nigra* forest plantation, planted in 1957, at Roggebotzand, The Netherlands. No understory vegetation was present. Further description of the site is given in Faber & Verhoef 1991. During the experiment weather conditions were mild and moist, typically for this temperature region with a maritime climate.

Experiment design and layout

Animal stratification was described using litterbags with fresh litter (L: 4 mm mesh, 3 cm thickness), fragmented litter (F: 2 mm mesh, 2 cm thickness), or humus (H: top 1 mm mesh, bottom 350 µm mesh, 1 cm thickness). All materials were defaunated following collection in the field, by drying at 40 °C. Litterbags were laid out on top of each other, in natural order, within enclosures on the forest floor. These enclosures (0.5 × 1 m) served to experimentally include or exclude soil fauna and tree roots, as described below. No aboveground vegation structures were present inside the enclosures. These treatments served to test whether the presence of other soil fauna and of roots affects the depth distribution of particular Collembola species. The soil fauna treatments consisted of the introduction of the Collembola *Orchesella cincta* (Linné), *Tomocerus minor* (Lubbock) and *Isotoma notabilis* Willem; also included was a soil fauna of natural diversity, collected by hand sorting of the organic layer at the site, and by Tullgren collections from soil cores. All animals were introduced into the enclosures, and could immigrate freely into the litterbags; mesh sizes reflected natural pore sizes. Roots were cut and absent in half of the plots, and were prevented from regrowing into the enclosures by stainless steel plates, dug into the ground to a depth of 1 m (Faber & Verhoef 1991).
Litterbags were used to facilitate the measuring of litter mass loss and the stratified sampling of soil fauna, using the same sample. Litter leachates were sampled, using vacuum tube lysimeters, in a study of the impact of tree roots on soil water acidity, and the relationship with microstratification of Collembola. Experiment design and the layout of enclosures, litterbags, and lysimeters, are described in detail in Faber & Verhoef 1991. Litterbags were sampled twice a year: in winter (3 occasions) and in summer (2 occasions), from 1987 to 1989. Collembola were extracted using Tullgren apparatus, and killed and preserved in Gisin's fixative (1960). Animals were counted and body lenghts were measured under a dissecting microscope at magnification 25 ×. The method was reliable to a 0.04 mm interval. Body lengths of entomobryid and isotomid species were determined as the distance from the anterior of the second thoracic segment and the posterior of the fifth abdominal segment. Sminthurid, onychiurid and podurid species' body lenghts were determined from the frons to the posterior of the fifth abdominal segment. Measurements were not corrected for preservative induced swelling of animal bodies (Petersen 1975).

Measurement of microstratification

Measurement of depth distribution of the Collembola follows Usher 1970. Litterbags that were superposed on each other were considered to be subsamples of a soil core. Thus, the number of animals in the core, N, equals the sum of the numbers n in the respective litterbags L, F, and H:

$$N = n_L + n_F + n_H,$$

the weighed average, or 'mean depth', M, is

$$M = (d_L \cdot n_L + d_F \cdot n_F + d_H \cdot n_H) N^{-1},$$

and the 'depth deviation', S, a measure of variation around the mean depth is

$$S = \sqrt{\{(n_L(d_L - M)^2 + n_F(d_F - M)^2 + n_H(d_H - M)^2) N^{-1}\}}.$$

in which d is the centre of depth of a particular litterbag. As the amount of litter in the litterbags declines with time, d also decreases. The use of the litterbag technique would thus obstruct any comparative study of data from different sampling periods, or of data from studies using subsamples with different centres of depth. The litterbag centres of depth were converted to relative measures, so: $d_L = 1$, $d_F = 2$, and $d_H = 3$. As a result of this conversion, estimates were obtained for the mean relative depth M, and the relative depth deviation S; these may have greater potential for studies using a comparative approach. Relative depth can be transformed back to "actual" depth for a particular organic soil layer, when the total thickness of the organic layer, h, and the centres of depth of L, F, and H-horizons are known:

transformation factor $= (d_L + d_F + d_H) h^{-1}$.

In the present observations, the average transformation factor was set 1.7, and was based on an initial total thickness of 6 cm for the organic layer, and a thickness of 4 cm at the final observations.

Statistics

The mean depth and depth deviation of individual Collembola species were analyzed for the effects of the presence of tree roots and other soil fauna species, for single sampling periods, using two-way analysis of variance (ANOVA). ANOVA procedures for repeated measures were used, when data sets for the entire experiment were studied (Sokal & Rohlf 1981). This technique was also used to test the effect of leachate pH on depth distribution of the animals. Unplanned comparisons between means of specific mean depths and depth deviations under various soil fauna treatments were subsequently evaluated, using the Student-Newman-Keuls test. The experimental error or the protection level for the collection of all tests made, was fixed at $\alpha_E = 0.05$ (Winer 1971, p. 196). The relationships between litter moisture and mean depths of Collembola species were characterised by means of model I regression analysis. The relationships were established for prediction purposes only, and were not interpreted as functional relationships (Sokal & Rohlf 1981, p. 549). The multiple R (in these cases the Pearson correlations, with coefficient r) were tested for significance by a two-tailed t-test. All tests and correlations were provided by SYSTAT version 3.2 (Wilkinson 1987). Levels of significance are indicated as * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$; correlations between variables were considered significant when $P \leq 0.01$.

Results

During the 2.5-year field sampling program some 15 species of Collembola were recovered from the litterbags at 6-months sampling intervals. Only seven species were sufficiently abundant to facilitate the calculation of their mean relative depth (M) and the relative depth deviation (S) with acceptable statistical reliability. The results are presented in Table 1, in which the nomenclature follows Fjellberg 1980. The number of animals varied in time, numbers of $O. cincta$ and $T. minor$ declined during the experiment, while $Neelus$ $minimus$ (Willem) increased in number. Low total numbers of individuals implied low numbers of cases, which may then have biased estimations for M and S. Collembola species were ranked by average M, and specific mean relative depths could be recognized (Fig. 1). During the experiment, $O. cincta$ exhibited a lifestyle closest to the soil surface, while $Neanura$ $muscorum$ (Templeton) was the most deep-living species. The average depth deviation differed amongst species, and varied between 0.2 and 0.6 cm, which is equivalent to $0.4 - 1.2$ cm in a 6 cm thick organic layer with $L : F : H = 3 : 2 : 1$ cm structure (conversion factor $= 1.7$).

Further data on microstratification of Collembola species and factors of potential effect are presented below.

Table 1. Seasonal variation in mean relative depth (cm), relative depth deviation (cm), number of statistical cases and total number (100 cm^{-2}) of individuals of Collembola species, captured during the sampling period. Species are ordered by average mean relative depth

Variable	Sampling occasion					Statistic
	January 1987	August 1987	January 1988	August 1988	January 1989	
Mean relative depth (M)						weighed average
Orchesella cincta (L.)	1.35	1.17	1.50	1.37	1.22	1.29
Tomocerus minor (Lubbock)	1.51	1.18	1.33	1.49	1.38	1.37
Lepidocyrtus lignorum (Fabricius)	1.71	1.43	1.38	1.58	1.34	1.45
L. cyaneus Tullberg	1.35	1.56	1.55	1.52	1.49	1.50
Isotoma notabilis Schäfer	1.41	1.63	1.59	1.47	1.72	1.57
Neelus minimus (Willem)	–	–	1.71	1.60	1.65	1.62
Neanura muscorum (Templeton)	1.67	1.47	1.87	1.71	1.55	1.67
Relative depth deviation (S)						weighed average
O. cincta	0.36	0.28	0.00	0.32	0.00	0.29
T. minor	0.32	0.37	0.48	0.47	0.39	0.41
L. lignorum	0.00	0.28	0.33	0.46	0.30	0.33
L. cyaneus	0.05	0.23	0.16	0.13	0.21	0.17
I. notabilis	0.38	0.64	0.53	0.57	0.66	0.56
Ne. minimus	–	–	0.04	0.39	0.38	0.33
N. muscorum	0.00	0.20	0.14	0.29	0.24	0.21
Number of cases						sum
O. cincta	44	44	2	28	9	127
T. minor	30	48	47	47	47	219
L. lignorum	7	42	43	48	43	183
L. cyaneus	10	34	18	22	20	104
I. notabilis	42	48	48	48	48	234
Ne. minimus	0	0	12	26	44	82
N. muscorum	3	17	36	34	29	119
Number of specimens						sum
O. cincta	763	706	2	399	11	1881
T. minor	2490	3286	3475	1106	1161	11518
L. lignorum	9	275	287	925	185	1681
L. cyaneus	15	143	84	96	90	428
I. notabilis	747	7544	1256	1821	3011	14379
Ne. minimus	0	0	82	1387	11029	12498
N. muscorum	6	114	262	125	115	622

– No animals captured

Fluctuations in time

With the exception of *Lepidocyrus cyaneus* Tullberg and *Ne. minimus*, all Collembola species (Table 1) showed variable mean relative depths during the sampling program ($2.472^* \leq F \leq 8.262^{***}$): the depth deviations of *O. cincta*, *T. minor*, *I. notabilis* and *Lepidocytus lignorum* (Fabricius) also differed with time ($5.290^{***} \leq F \leq 17.349^{***}$). These variations did not show seasonality between winter and summer samplings, or consistency among species.
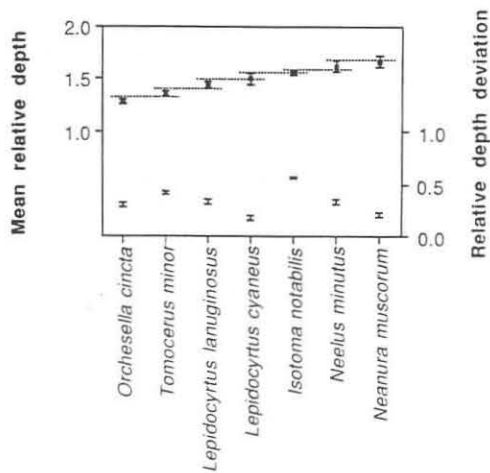
Fig. 1. Microstratification and spatial variation of some Collembola species during a 2.5 year field study, expressed as average mean relative depth (cm) and average relative depth deviation (cm). Means with standard errors: means joined by a hatched line were not significantly different at $\alpha = 0.05$

Body length

Using data of all samplings, the specific microstratification of Collembola was described as a function of individual body length. As indicated in Fig. 2, the adults of most species were found higher up in the soil profile, while hatchlings and juveniles were captured at depth. *T. minor* and *N. muscorum*, however, showed little relationship between the mean relative depth and body length. Some adults were occasionally found in deeper layers, but their actual numbers were relatively small.

As illustrated in Fig. 3, the relative depth deviation of individuals ranged between 0.3–0.8 mm for most body lengths. It is noteworthy, that maximum depth deviation was found with juveniles, and that very little depth deviation was recorded for the bigger individuals, suggesting low vertical mobility of adult animals.

In conclusion, juvenile Collembola were generally found in the deeper soil layers and exhibited greater depth deviation than adults. Vertical distribution patterns could not be predicted from body length, however, as the relationship of body length to mean relative depth and depth deviation varied among species.

Population density

The relationships between population densities of Collembola species and their mean relative depth and depth deviation were studied, using the data of all samplings. The Pearson product moment correlation coefficients are presented in Table 2. For *L. lignorum*, the mean relative depth increased with population density; within the observed ranges of population density, with a maximium observed density of N_{max}, no significant relationships were found for other species. The depth deviation of all species investigated increased with animal density, with the exception of *N. muscorum*.

Soil moisture

The relationship of the vertical distribution of Collembola species to litter moisture was investigated using data from the entire 2.5-year study period. The cases that rendered values for *M* or *S* equalling steps of 0.5 cm are omitted, as these resulted from low animal numbers.

and imply biased relationships. The coefficients for the Pearson correlations are presented in Table 3. The mean relative depth of *O. cincta* and *T. minor* decreased with the moisture content of the organic layer; further analysis revealed that these relationships were predominantly based on moisture contents of fresh and fragmented litter. The relative depth deviation of these species also decreased with the moisture content in the litter layers. Contrastingly, with increasing moisture in the fragmented litter layer, *Ne. minimus* was found deeper in the soil profile, the depth deviation of the animals was not significantly affected. Humus moisture content affected depth deviation for *L. cyaneus* and *I. notabilis*, but no impact on the mean relative depth of these species was registered.
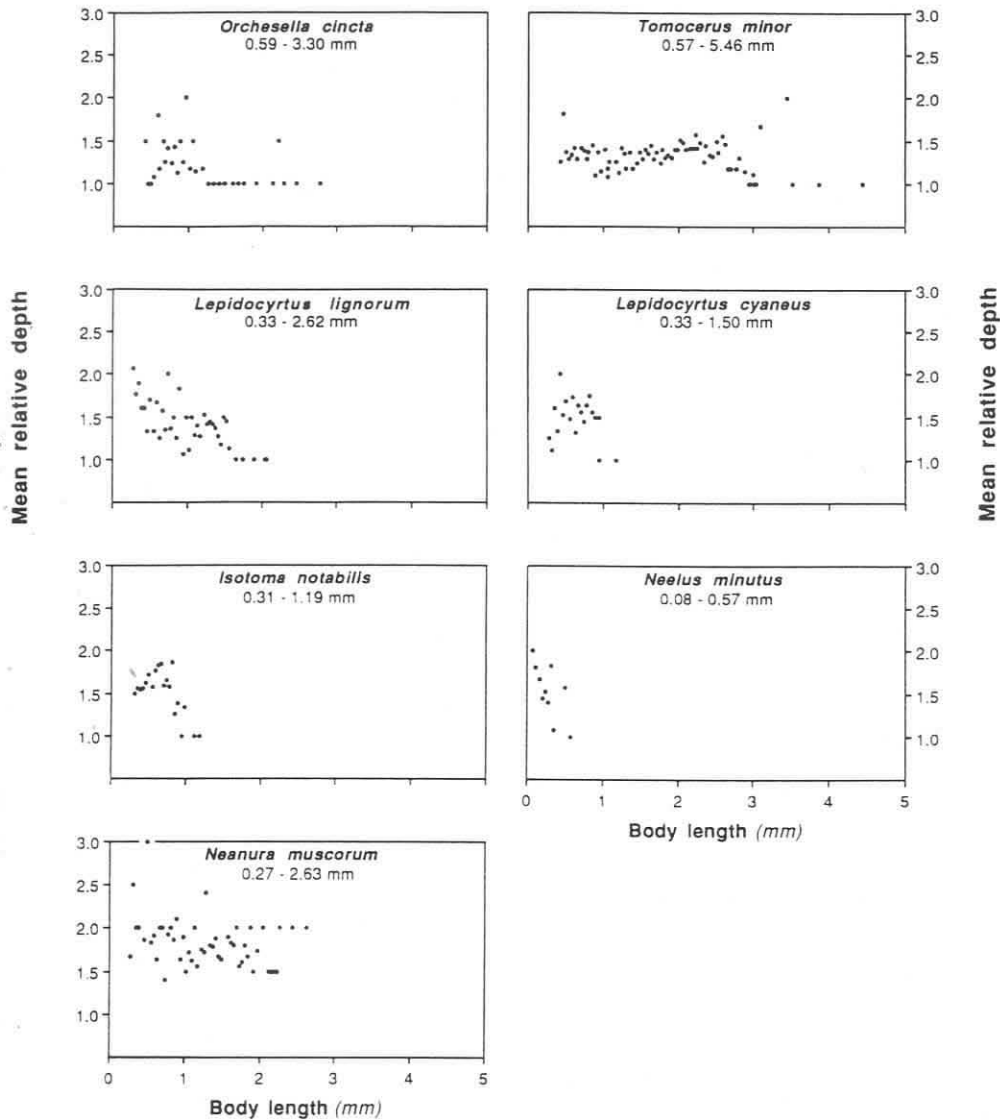

Fig. 2. Overall mean relative depth (cm) of some Collembola species during a 2.5-year field study, in relation to body length. Note different measures for body length between species (see methods). The observed ranges for total body lengths including headcapsules are given

The microstratification of some Collembola species was found to be affected by the presence of live pine roots, when data for the entire 2.5-year sampling period were compared (Fig. 4). Individuals of *L. lignorum, I. notabilis* and *Ne. minimus* showed smaller mean relative depths in the presence of roots than in their absence (Fig. 4A). For *L. lignorum* this concurred with a decreased relative depth deviation (Fig. 4B). The stratification of other species did not respond to tree root manipulation. The effect of soil water acidity on microstratification of Collembola species was investigated in relation to tree roots. The pH of the organic layer leachate fluctuated in time ($F_{4, 164} = 96.414***$), and after 10 months was higher in
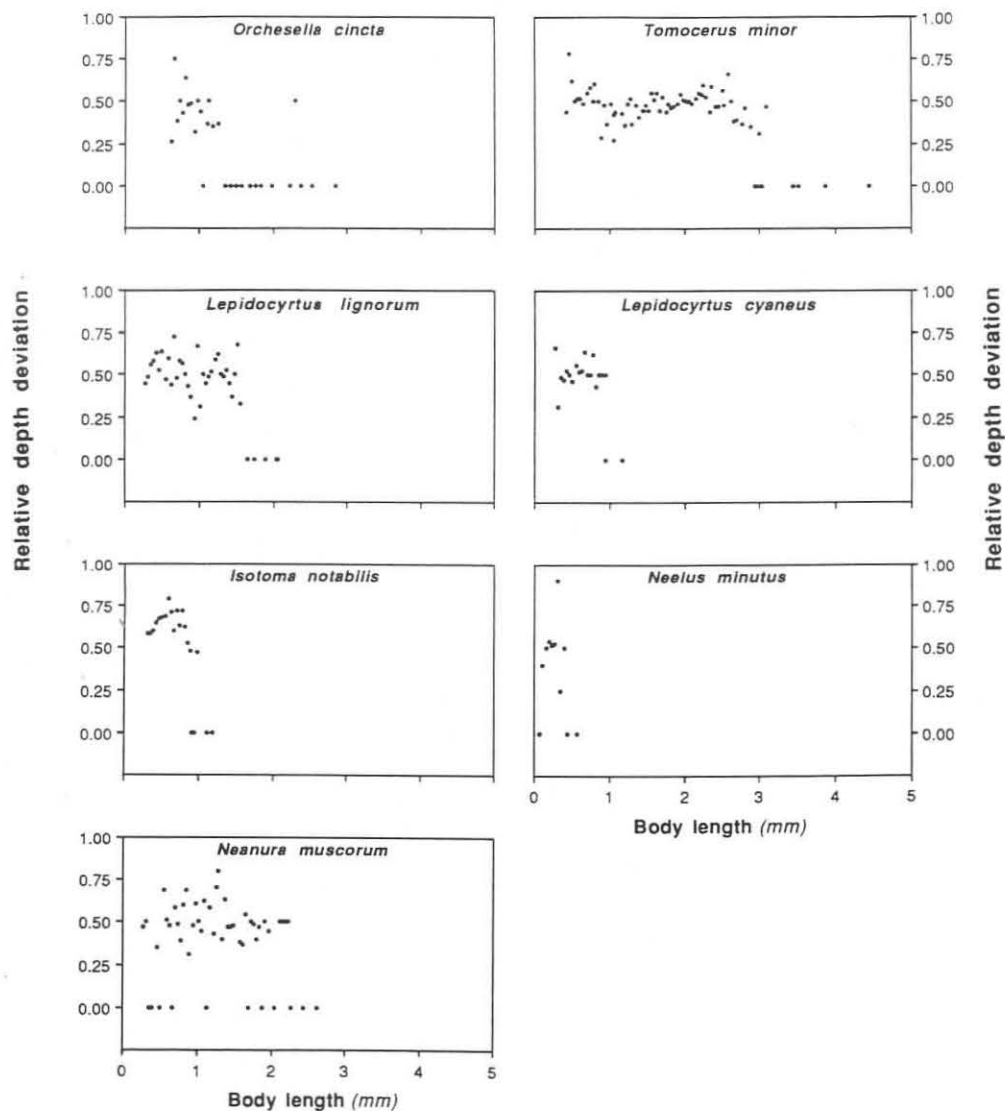

Fig. 3. Overall relative depth deviation (cm) of Collembola species in relation to body length. See legend to Figure 2

Table 2. Pearson correlation coefficients for relationships of population density with mean relative depth (M) and depth deviation (S) of some Collembola species. The number of observations (n) and maximum observed density per sample (N_{max}, numbers $100\ cm^{-2}$) are given: correlations were considered significant when $P \leq 0.01$

Collembola species	M	S	n	N_{max}
Orchesella cincta	0.005	0.365***	127	99
Tomocerus minor	−0.131	0.244***	219	343
Lepidocyrtus lignorum	−0.206**	0.232**	183	155
Lepidocyrtus cyaneus	−0.032	0.356***	104	34
Isotoma notabilis	−0.123	0.173**	234	1408
Neelus minimus	−0.143	0.310**	82	1209
Neanura muscorum	−0.069	0.220	119	65

rooted plots than in non-rooted plots ($F_{1,41} = 7.208$**). When overall data were analysed. no correlations were established for leachate pH with mean relative depth of Collembola species. except for a negative relationship for *N. muscorum* ($r = -0.280$**). The relative depth deviation was positively related to leachate pH in the case of *Ne. minimus* ($r = 0.465$***). and negatively for *T. minor* ($r = -0.223$***). No relationships could be established for other species.

The water content of the organic layer was effected by tree roots in the samplings of summer 1988 and winter 1989. when rooted plots were dryer than non-rooted plots ($F_{4,227} = 9.946$***).

Interspecific relationships

The experimental manipulation of the presence of soil fauna enabled the testing of interspecific relationships affecting the vertical distribution of Collembola species. Using
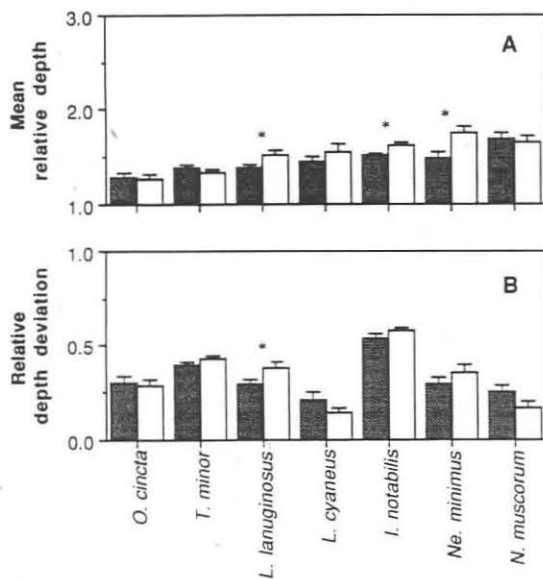

Fig. 4. Mean relative depth (A. in cm) and relative depth deviation (B. in cm) of some Collembola species in relation to the presence (filled bars) or absence (white bars) of live pine tree roots. Means with standard errors. Collembolan genera: O = *Orchesella*; T = *Tomocerus*; L = *Lepidocyrtus*; I = *Isotoma*; *Ne* = *Neelus*; *N* = *Neanura*

Table 3. Relationships of mean relative depth and relative depth deviation of some Collembola species with moisture content in fresh litter (L), fragmented litter (F), humus (H), and total organic layer (Σ). Pearson correlation coefficients are given; correlations were considered significant when $P \leq 0.01$

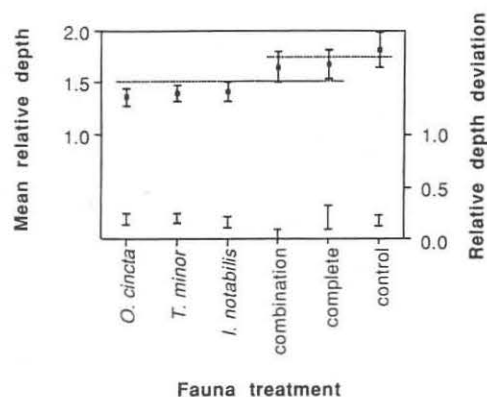| Collembola species	Mean relative depth				Relative depth deviation			
	L	F	H	Σ	L	F	H	Σ
Orchesella cincta	−0.415***	−0.150	−0.193	−0.292**	−0.503***	−0.316**	−0.195	−0.426***
Tomocerus minor	−0.413***	−0.256***	−0.136	−0.317***	−0.361***	−0.177	−0.094	−0.237**
Lepidocyrtus lignorum	−0.087	−0.057	0.138	−0.021	−0.005	0.016	0.058	0.041
Lepidocyrtus cyaneus	−0.191	−0.077	0.109	−0.038	−0.187	−0.230	−0.498**	−0.415
Isotoma notabilis	0.126	0.094	0.130	0.143	0.102	0.076	0.196**	0.129
Neelus minimus	0.121	0.438***	0.264	0.411**	−0.098	0.091	0.104	0.037
Neanura muscorum	0.043	0.040	−0.064	0.044	−0.253	−0.179	−0.072	−0.186

Fig. 5. Mean relative depth (cm) and relative depth deviation (cm) of *Lepidocyrtus cyaneus* as affected by soil fauna manipulation. Means with standard errors; means joined by a hatched line were not significantly different at $\alpha = 0.05$

ANOVA of the data for the entire sampling period. soil fauna manipulation was demonstrated to affect the mean relative depth of *L. cyaneus* ($F_{5,99} = 2.806^*$, Fig. 5). *L. cyaneus* was found more superficially in the soil profile in the presence of a second Collembola species. be it either *O. cincta*, *T. minor* or *I. notabilis*, than in absence of soil fauna. Relative depth deviation was not affected. No effects were observed for the other Collembola species under investigation.

Discussion

Methodology of measurement of vertical distribution

The measurement of the vertical distribution of soil fauna. using the statistics M and S. enables a comparison of the depth of populations sampled at different times of the year. or at different places (Usher 1970: Takeda 1978: Kampichler 1990). We suggest the use of relative measures to facilitate these comparisons. complying with Christiansen's (1964) plea to present metric depths and to aim to detect relationships between soil fauna and soil strata. In the present study. M varied between 1.0 (all animals in the fresh litter layer) and 3.0 (all animals in the humus layer). Values lower than 1.0 are conceivable. if epigeic and hemiedaphic species are sampled from aboveground vegetation. The vertical migration of Collembola between soil and vegetation may be of considerable importance to soil population densities. as tree climbing behaviour is induced by conditions of high air humidity (Bauer 1979). Likewise. values for M higher than 3.0 can be obtained. especially for euedaphic species. when sampling deeper cores including mineral soil layers. Thus. observed values for M are likely to show variation over a greater range. with greater differences between species. when sampling all habitat strata within the ecosystem.

One should be careful when using M and S for a description of vertical distribution characteristics. when attemiting a correlation between the two statistics. As the core is subsampled. values for both M and S show discrete variation at low animal densities in the soil core. Given that S is a function of M. the minimum value of S is related to M: when M varies between the centres of depth of subsamples. S cannot amount to less than an absolute value that is described by a series of semicircles. with diameters equalling the subsample depth or ranking step value, and centering at the respective subsample depths
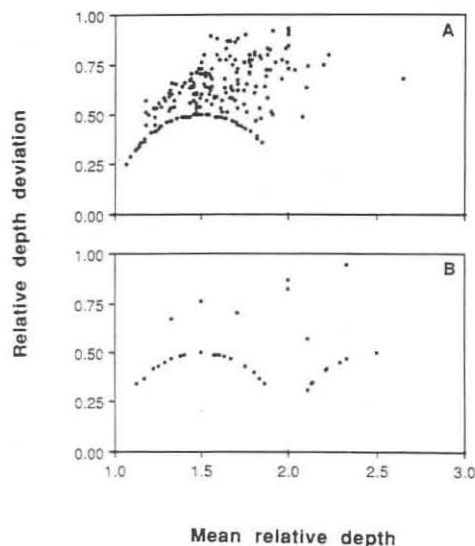
Fig. 6. Relationship between mean relative depth (cm) and relative depth deviation (cm). A: *Isotoma notabilis* (n = 234). B: *Neanura muscorum* (n = 119)

or ranking values. This is exemplified in Fig. 6 for data on the relative depth distribution of two species of Collembola. In other words. S can only equal zero when $M = d_i + 0.5d_i$. and S_{min} increases with increasing absolute difference between W and the nearest d_i:

$$S_{min} \geq \sqrt{\{r^2 - (M - (d_i + 0.5r_i))^2\}} \, .$$

wherein S_{min} is the minimum value possible at a given value for M. d_i is the centre of depth of subsample i. and r_i equals half the thickness of subsample i or the ranking value minus half the ranking step value. Correlations between W and S are distorted, therefore. and we refrain from analysing the species specific relationships.

Vertical distribution

Previous studies indicated that the upper few centimeters of the soil profile generally support the highest numbers of Collembola (Hågvar 1983. and references herein). This choice of microhabitat is thought to be related to the sites where the most active decomposition of organic material occurs (Wallwork 1970. p 134). In podzol soils. the F-layer is particularly optimal for reasons of food abundancy. pore space suitability. and water holding capacity (Haarløv 1955). The present data show that the most abundant species occurring in the organic layer were predominantly found in the L-layer, and less in the F-layer, while only a few percent could be recovered from the humus.

The morphological classification of Collembola into life forms (Gisin 1943: 'Lebensformen') generally reflects the vertical distribution of species over the soil profile (Hale 1966; Hågvar 1983). while other phenological and physiological aspects of collembolan ecology are also related (Christiansen 1964: Petersen 1980). Seven species were sufficiently abundant to calculate depth distributions accurately at all sampling occasions, the results correspond with the view that epigeic life forms (Entomobryidae: *O. cincta*), if in the soil, are generally found in the top of the profile, while euedaphic forms (Poduridae: *N. muscorum*; Sminthuridae: *Ne. minimus*) are found deeper down, and hemiedaphic forms (Entomobryidae: *T. minor*. *Lepidocyrtus spp*: Isotomidae: *I. notabilis*) inbetween the former two

groups. Though most Collembola species investigated here showed considerable variability in their depth distribution, mean depths were shown to differ amongst species on a millimeter scale. These subtle differences in micro-distribution may well be a mechanism for avoidance of interspecific competition, representing a "single niche dimension" (cf. Jennings & Barkham 1979). Previously, resource partitioning through micro-habitat utilization at the level of organic soil layers was argued for by Takeda (1987). The present data indicate even finer segregation.

Life cycle aspects

Hatchlings and juveniles generally showed greater variability in depth of occurrence than adults. Similar observations have been made previously (Knight 1963), and the phenomenon may be explained to some extent by soil pore sizes restricting the mobility of the bigger individuals (Haarløv 1955, 1960). The apparently lower depths for hatchlings, as observed for *O. cincta*, *L. cyaneus* and *I. notabilis*, may be due to oviposition in a relatively superficial layer, and juveniles migrating downwards. Such observations have been reported for the collembolan *Tetracanthella sylvatica* (Takeda 1976). In addition, it seems likely that age specific water balances for the animals may also be explanatory; transpiration rates of Collembola were found to be strongly negatively related to body weight (Vannier & Verhoef 1978; Verhoef & Li 1983), with *O. cincta* showing a marked decline in response for body weights of around 0.2 mg dry weight (H. A. Verhoef, pers. comm.). This weight is equivalent to 1.9 mm total body length (Janssen & Joosse 1987), or 1.5 mm excluding the head capsule, well below the minimum adult total body length of 2.3 mm (Joosse & Veltkamp 1970). Variability in juvenile depth distribution may also been caused by life cycle related differences in food choice, as suggested for *Folsomia candida* (Bakonyi 1989).

Population density

Literature on the relationship between mean depth and population density is scarce. Usher (1970) reported for *Friesea mirabilis*, out of 7 Collembola species investigated, that with high densities the animals were found deeper in the soil profile. In the present study such a relationship could not be demonstrated for any species, except *L. lignorum*. It can be argued that a pseudo-correlation is involved here: a seasonal or microclimatic factor, other than soil moisture, may have caused variation to both mean depth and population density (Volz 1934; Dowdy 1944; Knight 1963; McBrayer et al. 1977; Persson & Lohm 1977). Further study of this relationship is needed.
Increasing animal densities resulted in higher depth deviations, or conversely, low densities concurred with low variation in depth distributions. These observations suggest that population size can affect intraspecific competition pressure.

Moisture

If correlations between depth of occurrence of Collembola species and the soil water content were demonstrated in the present study, they were weak, and although the experiment set up did not allow for a regression approach, it would seem that moisture was not a key factor in explaining the observed variation in mean depths of the Collembola. As expected, the relationships for *O. cincta* and *T. minor* were negative, corresponding to earlier observations that both species migrate downwards to avoid summer droughts (Verhoef & van Selm 1983; van der Woude & Verhoef 1986). Unexpectedly, *Ne. minimus* showed the reverse response in fragmented litter. A similar response was reported for the collembolan

Tullbergia callipygos in relation to rainfall (Usher 1970). As soil arthropods can be affected by soil moisture directly, and indirectly, through the availability of food (Hassall et al. 1986), the latter might have been the driving mechanism behind these observations.

Roots

The vertical distributions of soil microarthropods has been reported to coincide with root biomass in a shortgrass steppe (Leetham & Milchunas 1985). The present data demonstrate the effect of the presence of live tree roots, with associated mycorrhiza, on the vertical distribution of some, but not all Collembola species. When affected, the animals were collected higher in the soil profile than found in absence of roots. The effect is unlikely to be explained by root impacts on soil acidity, as the mean relative depths of species that were affected by root presence were not related to leachate acidity. The seasonally lower water content of the organic layer in rooted plots may have been a causal factor, but for *Ne. minimus* only, since this was the only species that established its depth in response to both tree roots and soil moisture. For *I. notabilis* and *L. lignorum*, also responding to tree roots, these explanations do not hold. Possibly, the response of these species originates from differences in availability of favourable food between rooted and non-rooted plots.

Interspecific relationships

With regard to vertical distribution, both positive and negative correlations between Collembola species have been reported previously (Poole 1961; Usher 1970). A complex network of interspecific relationships has also been suggested (Hågvar 1983). These studies involved a correlative approach. The present study indicates, through experimental manipulation, a response in microhabitat use by *L. cyaneus* in the presence of other Collembola species. It remains unclear whether this response results from competition between these species. Interspecific competition has been demonstrated by experimental manipulation for two Cryptostigmatid mites (Anderson 1978).

Concluding remarks

The results of this study show subtle specificity in depth distributions of litter dwelling Collembola. Since food resources and a number of edaphic factors are associated with depth, depth of occurrence of these animals can be considered a niche dimension. Niches may vary within species with life cycle, and between species with what is probably a complex set of biotic and abiotic factors, continuously changing with time. Individuals can progressively maximize their survival and reproductive efforts through vertical migration. At the species level, epigeic and hemiedaphic species particularly show swift and flexible responses to their dynamic environment (Wolters 1983). Consideration should be given to factors that determine the microhabitat choice of animals, when studying interspecific relationships in a community ecology approach, as well as when studying the role of soil fauna in decomposition processes in a systems ecology approach (Faber & Verhoef 1991).

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